

AFFINITY OF THE CAMBRIAN ALGA *TUBOMORPHOPHYTON* AND ITS SIGNIFICANCE FOR THE EPIPHYTACEAE

by ROBERT RIDING and LARISA VORONOVA

ABSTRACT. The problem of the true nature of the alga *Epiphyton* Bornemann and its allies centres upon the difficulty of recognizing features of affinity in these morphologically simple fossils. They have been compared with algae in a number of different groups, including, especially, florideophycidean rhodophytes. However, the general dimensions and shape of the Cambrian epiphytacean *Tubomorphophyton* Korde in specimens from Siberia suggest that it could be a bangialean rhodophyte, but details of its morphology and style of calcification are more consistent with its being a filamentous ensheathed cyanophyte. Its tubiform morphology is obscured in some specimens, probably due to the thickness of the calcified sheath material and to diagenetic alteration. This suggests that other epiphytaceans with apparently solid skeletons could be cyanophytes. Alternatively, the Epiphytaceae may be a heterogeneous group of algae superficially similar in gross morphology. These possibilities require reassessment of the nature and diversity of early Phanerozoic algal communities.

АННОТАЦИЯ. Проблема природы *Epiphyton* Bornemann и близких ему родов заключается в том, что в связи с простым морфологическим строением систематическая принадлежность их определяется с трудом. Размер и форма кембрийских *Tubomorphophyton* Korde в образцах из Сибири дают основание предполагать, что они могли быть филламентными (нитчатыми) цианобактериями или эукариотными водорослями. Размер, морфология и кальцификация *Tubomorphophyton* дают возможность их относить к филламентным (нитчатым) цианобактериям. Их трубчатая форма в некоторых образцах видна плохо скорее всего из-за толщины кальцифицированной оболочки, а это дает основание предполагать, что другие эпифитации, которые целиком состоят из микрочернистого карбоната, могли быть также скорее цианобактериями, а не родифитами, как обычно считалось. Но эпифитации также могли быть гетерогенной группой водорослей, различных по своей природе, но сходной по макроморфологии. Каждая из этих возможностей требует переоценки природы и разнообразия водорослевых сообществ раннего фанерозоя.

THE Epiphytaceae Korde is one of the most distinctive and widespread algal groups appearing in the Lower Cambrian. These small but heavily calcified fossils, which characteristically form dendritic thalli a few millimetres in size, are prominent in shallow marine limestones of Cambrian age in Antarctica (Priestley and David 1910), Australia (Walter 1967), Europe (Bornemann 1886), North America (Ahr 1971; Handfield 1971), and the Soviet Union (Vologdin 1931, Korde 1955, 1959, 1961, 1973; Krasnopeeva 1955; Gudymovich 1967; Luchinina 1975; Reitlinger 1959; Voronova 1976; Drosdova 1980). They are commonly major rock-builders and alone, or in association with other algae and archaeocyathans, are important elements of Lower Cambrian bioherms. *Epiphyton* occurs in the Middle Cambrian of the Siberian Platform (Korde 1955, 1961) and the Middle Cambrian of the Altai-Sayan foldbelt (Stepanova 1974). It is common in the Middle Cambrian Cathedral Formation of British Columbia (McIlraeth 1977, p. 116) and is present in the Lower Ordovician of Kazakhstan (Voronova 1980). *Epiphyton*-like fossils, possibly *Angulocellularia* Vologdin (Riding and Voronova, *in press*), also occur in the Lower Ordovician *Calathium*-*Archaeoscyphia* bioherms of the south-western United States (Riding and Toomey 1972). *Epiphyton* reappears in Devonian stromatopoid-dominated bioherms in several parts of the world (Chuvashov 1965; Antropov 1967; Wray 1977; Riding 1979a).

Although Bornemann's (1886) original view that *Epiphyton* is probably an alga has not been seriously questioned, there has been no general agreement concerning the particular group to which it belongs. Bornemann (1886, pp. 16-17) thought it might be a chlorophyte but Pia (1927, p. 39) regarded it as a cyanophyte within the Porostromata; a view which Maslov (1956) endorsed, although with some uncertainty. Korde (1959) placed *Epiphyton* in yet another major algal group, the Rhodophyta, on the basis of her recognition of cellular microstructure and sporangia in specimens from the Cambrian of the south-eastern Siberian Platform. However, reservations have been expressed concerning the interpretation of these features (Maslov 1962; Voronova 1976; Wray 1977, pp. 41-42) and uncertainty remains concerning the affinity of *Epiphyton*. Apart from Korde, previous workers have not regarded specific features of *Epiphyton* and its allies as being distinctive of a particular group but have relied only on very general features in suggesting to which algal group they may belong. We propose here that one member of the Epiphytaceae, *Tubomorphophyton* Korde, has a distinctive morphology which is comparable with some bangialean rhodophytes, but which is more consistent with a cyanophyte affinity. If this tentative interpretation is extended to the Epiphytaceae as a whole, then it has a significant bearing upon our understanding of the early history of Palaeozoic algae because it suggests that a major group, often previously thought to be rhodophyte, is cyanophyte. If, on the other hand, *Tubomorphophyton* is regarded as distinct from *Epiphyton* and its relatives, then the implication will be that the Epiphytaceae is not a homogeneous group and that the diversity of Cambrian calcareous algae is greater than currently believed.

THE EPIPHYTACEAE

Epiphyton was originally described from the Cambrian of Sardinia by Bornemann (1886). Korde (1959) erected the family Epiphytaceae, comprising *Epiphyton* and *Chabakovia* Vologdin, and later (1961) established many new *Epiphyton* species. Subsequently, Korde (1973, p. 159) raised several of these to generic level and recognized the following ten constituent genera within the Epiphytaceae: *Epiphyton* Bornemann, *Epiphytonoides* Korde, *Gordonophyton* Korde, *Kosvophyton* Korde, *Ludlovia* Korde, *Paraepiphyton* Wray, *Proninophyton* Korde, *Streptophyton* Korde, *Tharamia* Wray, and *Tubomorphophyton* Korde.

Although the external bushy form of these fossils is distinctly plant-like, internal features of the calcareous skeleton which could be used to narrow the range of possible affinities are either lacking or equivocal. To most observers the skeleton appears to have a micritic ultrastructure without any features which might provide clues to its relationships, although Rozanov (1979, fig. 2, pp. 68-69) has noted the similarity between the micritic ultrastructures of *Epiphyton*, *Renalcis*, and archaeocyathans.

However, one member of the group, *Tubomorphophyton*, while retaining a micritic wall-structure, has a distinctly tubiform morphology. This is an important departure from the morphology to be expected if the Epiphytaceae as a whole had a skeletal structure similar to that of extant calcareous rhodophytes, in which the walls of individual cells are calcified and the organization is pseudoparenchymatous.

Both Luchinina (1975) and Wray (1977, p. 42) have recently considered that *Epiphyton* could be a cyanophyte. We enter the debate concerning its affinity to revive the older, more specific, opinion of Pia (1927) that allies of *Epiphyton* could belong to the Porostromata. This was foreshadowed by Gordon (1920, p. 684) when he described *E. fasciculatum* from the Antarctic as consisting of 'bifurcating tubules' and compared it with *Ortonella*. But, by basing our case on *Tubomorphophyton*, we believe it is stronger because, whereas most epiphytaceans are not clearly hollow, this genus has, as its name implies, a tubiform morphology comparable with that of filamentous cyanophytes, although it also resembles some rhodophytes. The problematic Reitlingerellidae (Loeblich and Tappan 1964, p. C787) is a group of tubiform calcareous microfossils but none of its members is comparable in form with *Tubomorphophyton*.

TUBOMORPHOPHYTON

All epiphytaceans show the dendritic form characteristic of the group, but their internal morphology ranges from rounded chambers and stacked discs to tubiform or apparently solid (Voronova 1976, fig. 21). To these features may be added the micromorphological details discerned by Korde (1959).

Tubomorphophyton is based on *E. botomense* Korde (1955) and the other members of the genus, *T. benignum*, *T. cristatum*, and *T. nubilum*, were also originally (Korde 1961) *Epiphyton* species prior to the erection of *Tubomorphophyton* (Korde 1973, p. 204). The feature which they share, and which distinguishes the genus, is the tubiform structure of the branches, although it should be noted here that the holotype of *T. benignum*, illustrated by Korde (1959, pl. 1, fig. 5) fails to show this character.

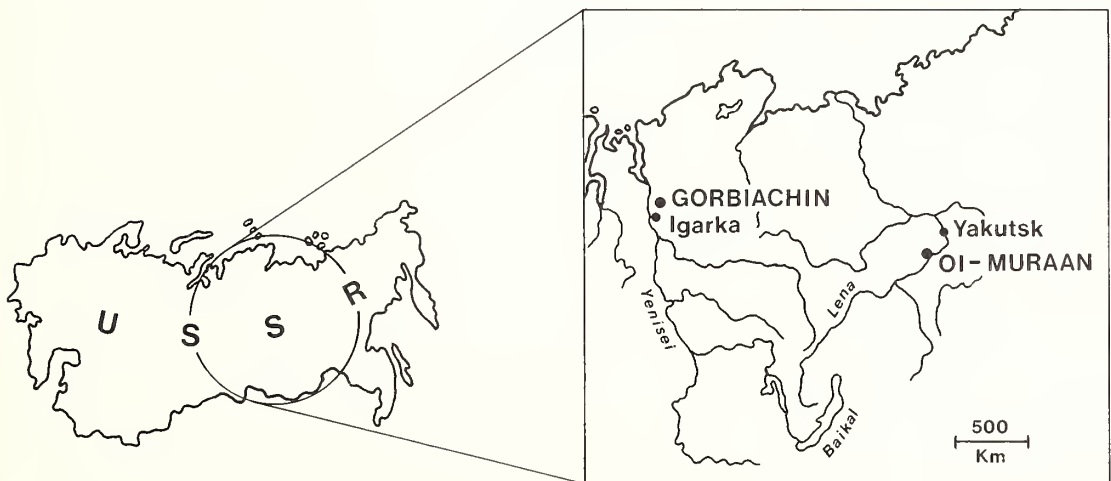
Tubomorphophyton has, so far, only been recorded from the Lower Cambrian of central and northern Asia. Korde (1973) describes it from the Lena River, Siberia, upstream from Yakutsk, and from the Kuznetskii Ala-Tau Mountains of the south-western Siberian Platform. The material described below is also from the Lena River and from a tributary of the Yenisei River further west.

Taxonomy

Korde (1961, 1973) has separated epiphytacean species on the basis of degree of branching, the angle and length of branches, the size of the thallus, and the diameter of filaments. In some cases the distinctions used are very fine and it can be difficult to satisfactorily follow the present taxonomy, a point which has been noted by Gudymovich (1967) and Luchinina (1975). The established species of *Tubomorphophyton* are so few in number (four) that they are easier to deal with: *benignum* and *cristatum* are relatively large forms and *cristatum* produces regular tufts branching at a low angle from the vertical; *botomense* has a slightly larger angle of branching; *nubilum* is a small form.

Material

The specimens described here are from the Lena and Gorbiachin Rivers of Siberia, USSR (text-fig. 1). They are of Lower Cambrian age, occurring in the Tommotian and Atdabanian Stages (text-fig. 2). The thin sections in which they occur are in the collections of the Palaeontological Institute (PIN) of the USSR Academy of Sciences, Moscow. Specimen B 927 (collection L. G. Voronova) is from the Gorbiachin River, a minor right-bank tributary of the Yenisei, and is of upper Tommotian age from the Krasny Porog Formation. Specimens B 70/25 and B 70/31 (collection L. G. Voronova) are from Oi-Muraan, a locality on the left bank of the Lena River, 3 km upstream from the village of Oi-Muraan (see Voronova 1976, p. 46 and fig. 23). This locality is between Zhurinsky Mys and Achehagy-Kyyry-Taas (see Cowie and Rozanov 1974, fig. 1). Specimen B 70/25 is of lower Atdabanian age from the Petrotsvet Formation. Specimen B 70/31 is also of Atdabanian age from the overlying Perekhod Formation.



TEXT-FIG. 1. Localities: Lena and Gorbiachin Rivers, Yakutia.

	TIME UNITS	LOCALITIES	
		Oi - Muraan	Gorbiachin
CAMBRIAN	Atdabanian	PEREKHOD ● B 70/31	KRASNY POROG ● B 927
		● B 70/25 PESTROTSVET	
	Tommotian		
PR	Yudomian	YUDOMA	SUKHARIKHA

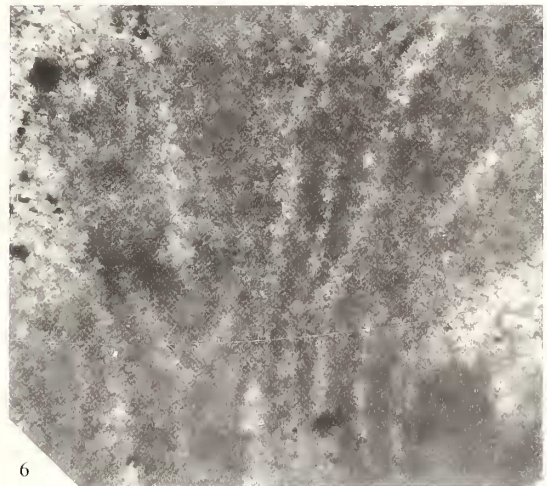
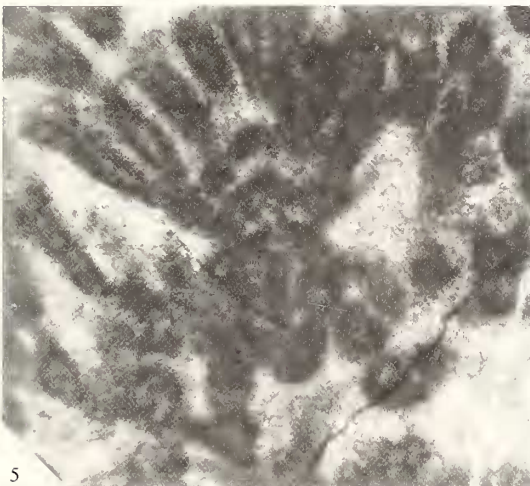
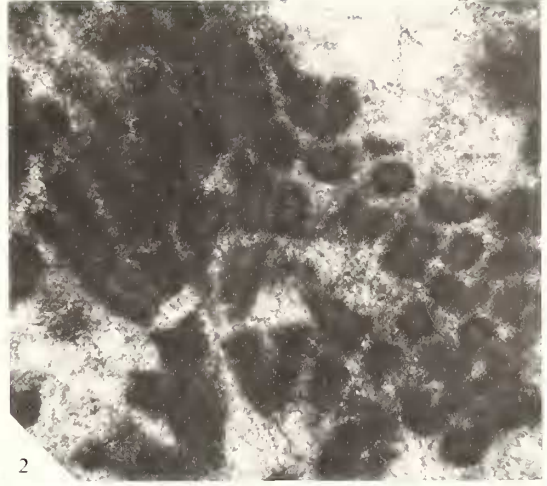
TEXT-FIG. 2. Stratigraphic position of the samples described here containing *Tubomorphophyton*. B 70/31 and B 70/25 both contain *T. botomense*. B 927 contains *T. benignum*. The Tommotian is currently regarded as the basal stage of the Cambrian, according to the preliminary recommendations of the International Working Group (Cowie 1978).

Morphology and dimensions

The specimens of *Tubomorphophyton* which we have examined are erect plants with short branches arising dichotomously and closely spaced to produce a dense tufted appearance (Pl. 96, fig. 1). There is no indication of a main axis. The filaments are of approximately constant diameter and are commonly seen to be hollow. The wall ranges in thickness from 3 to 34 μm , while the total tube diameter ranges from 23 to 91 μm . The tubular structure is seen most clearly in transverse sections (Pl. 96, fig. 2); in longitudinal sections the thickness of the wall, the thickness of the thin section, and the changing orientation of the skeleton combine to obscure the hollow interior, although this is nevertheless seen clearly in some specimens (Pl. 96, figs. 3, 4). In some cases the tube appears to close and reopen along the length of the filament, and branches with well-defined tubiform structure are juxtaposed against others which appear diffusely solid (Pl. 96, fig. 5). Our material contains both *T. botomense* (B 70/25 and B 70/31, Oi-Muraan) and *T. benignum* (B 927, Gorbiachin), the latter being distinctly larger. The fine structure of the skeleton appears to be featureless micrite (Plate 96, fig. 6). The tube interior is occupied by fine microsparite crystals.

EXPLANATION OF PLATE 96

Figs. 1-6. *Tubomorphophyton botomense* (Korde). 1, 3, 4, 6, sample PIN B 70/31, Perekhod Formation, Atdabanian; Oi-Muraan, Lena River, Siberia. 2, 5, sample PIN B 70/25, Pestrotsvet Formation, Atdabanian; Oi-Muraan, Lena River, Siberia. 1, longitudinal section showing tufted branched form of thallus, $\times 75$. 2, transverse and oblique sections showing hollow interior of tube, $\times 75$. 3, longitudinal section of individual branched tuft, $\times 85$. 4, detail of 3 showing tubiform nature of filaments, $\times 215$. 5, longitudinal, oblique, and transverse sections of filaments showing the variable preservation of the tubiform morphology, $\times 75$. 6, longitudinal section showing micritic microstructure of skeleton; note how tubes become obscure upwards, $\times 190$. All are uncovered thin sections.



DISCUSSION

Morphology

Korde (1973) considered *Tubomorphophyton* to be composed of a series of filaments, the 'wall' consisting of filaments more densely packed than those near the centre. In this she believed it to differ from *Epiphyton*, consisting throughout of densely packed filaments, and from *Gordonophyton* whose stacked branches she interpreted as reflecting alternating layers of vertically (light) and horizontally (dark) arranged filaments. We cannot confirm the presence of minute filaments within *Tubomorphophyton* and have only observed uniform micrite in the walls of the tube without any indication of distinctive ultrastructural features.

The tube diameter of *Tubomorphophyton* is comparable to, or slightly greater, than that of porostromates such as *Girvanella* Nicholson and Etheridge and *Ortonella* Garwood, but its wall is normally considerably thicker. In the *Tubomorphophyton* described here the ratio of total wall thickness to tube diameter is generally of the order of 2:3 compared with 1:2 for *Girvanella* (Riding 1977, p. 38) and in thin section specimens of *Tubomorphophyton* are not always obviously tubiform. We regard this as being primarily a reflection of original sheath thickness relative to filament diameter but both filament orientation in thin section and diagenetic modification of skeletal structure contribute to the clarity or otherwise of this feature.

The regular, abundant production of separate branches in *Tubomorphophyton* is similar to that of other epiphytaceans and distinguishes the group as a whole from unbranched or only very occasionally branched forms (*Girvanella*, *Proaulopora*) on the one hand, and from genera with closely appressed filaments (*Hedstroemia* Rothpletz, *Apophoretella* Elliott) on the other.

Affinity

In common with *Epiphyton* and *Gordonophyton* Korde (1973) recognized terminal sporangia in *Tubomorphophyton* and placed all three genera in the red algae under the Epiphytaceae. Most other recent workers have not expressed any confident or specific suggestions concerning the affinity of the group although Luchinina (1975) compared *Epiphyton* with *Rivularia*.

Morphologically, *Tubomorphophyton* somewhat resembles the extant porphyridiacean red alga *Goniotrichum* and similar comparisons can be made with filamentous chlorophytes. This raises the problem, constantly faced in work on fossil calcareous algae, of the significance to be attached to purely morphological similarities between uncalcified Recent forms and calcareous fossils. No calcified Recent filamentous rhodophytes are known to us; calcareous red algae at the present day comprise relatively complex forms such as Corallinaceae, Squamariaceae, and the chaetangiacean *Galaxaura*. These are marine and rhodophytes are uncommon in freshwater habitats at the present day. If red algae were more widely distributed in freshwater environments it is quite possible that they would calcify in tufa deposits, where carbonate deposition on plants occurs much more readily than in the sea. In such a situation calcareous filaments could be produced which might resemble *Tubomorphophyton*.

So, there are two courses open to us: we can either limit comparisons to only extant calcareous forms, or we can open up all the possibilities with the question 'if this soft alga happened to calcify, would it produce a skeleton similar to such-and-such a fossil?' Not only does the first course offer an easier approach, it also has the advantage of providing a more convincing basis for comparison; algal calcification may depend in some cases on environmental controls, but on the whole it is limited to particular groups and it is more plausible to compare fossil calcareous algae with extant calcareous forms than with non-calcareous groups. However, the present is not such a comprehensive key to the past; groups become extinct and habitats may change. In order to take these factors into account it is necessary to consider the second course of action, and to compare extant non-calcified forms with calcareous fossils, while still remembering that this difference does weaken any overall similarities which might otherwise occur.

Filamentous forms exist in a wide range of algal groups: cyanophytes, chlorophytes, rhodophytes, and phacophytes all have numerous examples of this type of organization. The only way to narrow

the field of possibilities is to emphasize the particular features of *Tubomorphophyton*: its small size and distinctive morphology.

The Recent small phaeophycean *Ectocarpus* has filament diameters of the order of 25–70 μm (Cardinal 1964), which places it in the same size range as *Tubomorphophyton*, but it has a main axis with lateral branches and also bears numerous reproductive bodies which might be preserved in fossils.

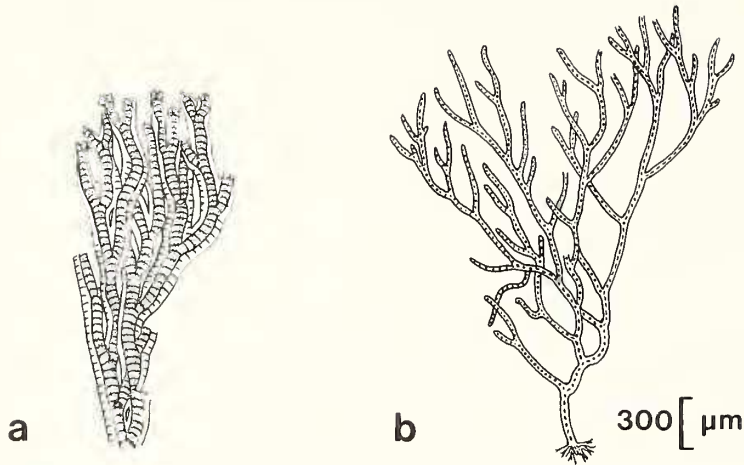
The Nemalionales (Rhodophyta) has a number of small, branched, filamentous forms (see Kylin 1956, pp. 87–88). *Kylinia* is up to about 2 mm high, *Audouinella* is 2–5 mm, and *Acrochaetium* also reaches 5 mm in height. But these genera also have main axes with lateral branches and the overall form does not closely resemble *Tubomorphophyton*.

Tubomorphophyton has a dichotomously branched form, without main axes being developed, and we have seen no spermatangia-like bodies preserved on it. Somewhat closer similarities exist between it and a small cladophoran species, perhaps, than with phaeophytes or rhodophytes. The chlorophyte *Cladophora pygmaea* reaches a height of only 1.0–1.33 mm, even in the adult, and individual filaments are up to 65 μm in diameter (Hoek 1963, pp. 36–37). But even though the gross form of this species resembles that of *Tubomorphophyton*, *C. pygmaea* also tends to show the development of a main axis, and another difference is that the diameter is distinctly variable along a filament (Hoek 1963, pl. 2, fig. 21), which is not the case with *Tubomorphophyton*.

Although none of these examples of eukaryotic algae is known to calcify, it is worth considering whether calcification, if it did occur, would produce a skeleton similar to that of *Tubomorphophyton*. Since *Tubomorphophyton* is a tube, calcification of such eukaryotes would have to be localized on the filament surface: if it were internal it would presumably affect cell walls and produce septa-like cross-partitions of the calcareous tube. Only by being external could it give rise to the simple morphology seen in the fossil. But *Tubomorphophyton* has a limit to its wall thickness, even though it is thick-walled by porostromate standards. The limitation on wall thickness in porostromates such as *Girvanella* and *Ortonella* is imposed by the sheath: it is the sheath which is calcified and sheath-thickness thus determines wall-thickness of the fossil. It is difficult to see how a similar constraint could be imposed on the thickness of an external calcareous layer of *Cladophora*, for example, since there is no distinct sheath present. In fact, calcification of much larger specimens of *Cladophora* has produced tubes in which the wall-thickness is very variable, the tubes, in many cases, being virtually transformed into solid rods (Riding 1979b).

But tubiform fossils of the simplicity and size of *Tubomorphophyton* do resemble Recent calcareous cyanophytes in which impregnation by CaCO_3 crystals preserved sheath-thickness, diameter, and form (Riding 1977, fig. 1). Sheath character is variable in cyanophytes. In comparison with *Ortonella*, for example, *Tubomorphophyton* has a thicker wall and less clearly tubiform structure, which can be interpreted to reflect a thicker, perhaps more diffuent, sheath. But this does not detract from the comparison between *Tubomorphophyton* and cyanophytes. In fact the wall of *Tubomorphophyton* is relatively thin in proportion to total tube diameter when compared with, say, calcareous *Cladophora*, and this feature of a limitation on wall-thickness indicates that *Tubomorphophyton* was produced by calcification of organic material, such as mucous sheath, with a certain size, rather than by external, unlimited, deposition of CaCO_3 on the surface of a filament. This suggests that *Tubomorphophyton* is a cyanophyte and its size, between 20 and 90 μm , is also directly comparable with the external diameter of many cyanophyte sheaths. However, *Tubomorphophyton*'s repeatedly branched thallus with its dichotomous bifurcations is complex by cyanophyte standards. Nevertheless, a few genera do show this type of organization: the stigonemataleans *Loriella* and *Stauromatonema* show erect filaments with forked branching (Fritsch 1959, p. 848). *Stauromatonema* and some genera of the Pulvinulariaceae are markedly heterotrichous (showing prostrate system giving rise to erect growths), but *Loriella* (Fritsch 1959, fig. 328H) appears to be entirely erect and closely resembles *Tubomorphophyton* in form (text-fig. 3a).

However, another candidate for comparison is the porphyridiacean (bangialean) rhodophyte *Goniotrichum*. This is a minute branching epiphyte in which some species, e.g. *G. cornu-cervi*, are only up to 1 mm in height. *G. elegans* is taller, but the filaments are only up to 50 μm thick (Newton 1931,



TEXT-FIG. 3. *a*, *Loriella osteophila* Borzi (cyanophyte), size uncertain, from Fritsch (1959, fig. 328*h*), after Borzi. *b*, *Goniotrichum elegans* Le Jolis (rhodophyte) from Newton (1931, fig. 150*b*). The repeated forked branching of *Loriella* more closely resembles *Tubomorphophyton* than does the pseudo-dichotomous branching of *Goniotrichum*.

p. 246). The walls are thick and mucilaginous (Fritsch 1959, p. 427, fig. 143). The dimensions and general form of *Goniotrichum* are comparable with *Tubomorphophyton*, but *Goniotrichum* is described as being pseudo-dichotomously branched (Newton 1931, p. 246) and in detail its thallus does not closely resemble *Tubomorphophyton* (text-fig. 3*b*). Another difference is that extant bangialeans do not calcify, although the mucilaginous envelope of *Goniotrichum* could, possibly, provide a site for calcification in certain circumstances.

Korde's (1959) view of *Epiphyton* is that it is a florideophycidean, and so belongs in the same broad group as the Chaetangiaceae and Corallinaceae. Our conclusion is that although *Tubomorphophyton* may be compared in size and gross morphology with a number of extant eukaryotes, including particularly the rhodophyte *Goniotrichum*, in detailed form and style of calcification it can most closely be compared with cyanophytes, especially certain stigonemataleans.

This interpretation has to be tentative; there is so much loss of the type of information used routinely by phycologists to establish comparisons between algae that we are reduced to using features which are not usually diagnostic. Although the possibility that *Tubomorphophyton* is a eukaryote, particularly a bangialean rhodophyte, cannot be excluded, the weight of evidence, in terms of size, morphology, and calcification, suggests to us at present that it is more likely to represent a branched, filamentous cyanophyte.

The solid appearance of some other epiphytaceans could mask a filamentous organization, and the recognition here of a likely cyanophyte nature for *Tubomorphophyton* strengthens the need for re-examination of the affinity of the Epiphytaceae as a whole. This is especially important because of the early appearance of these organisms in the skeletal fossil record: whether they represent cyanophytes or rhodophytes, or are a heterogeneous group of look-alike dendritic fossils, is bound to have considerable bearing on our understanding of the diversity and ecology of early Phanerozoic life on carbonate shelves.

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ROBERT RIDING

Department of Geology
University College
Cardiff CF1 1XL
United Kingdom

LARISA VORONOVA

Institute of Palaeontology
Academy of Sciences
ul. Profsoyuznaya 113
Moscow
USSR

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